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PHYLOGENETIC CHARACTER RESPONSES FOR SHAPE COMPONENT VARIANCE DURING THE MULTIVARIATE EVOLUTION OF EULACHNINE APHIDS: REDESCRIPTION OF *PSEUDESSIGELLA* HILLE RIS LAMBERS (HOMOPTERA: APHIDIDAE: LACHNINAE)

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Abstract.—Although suitable for conventional taxonomic purposes, previous descriptions of the monotypic aphid genus *Pseudessigella* Hille Ris Lambers and its species *Pseudessigella brachychaeta* Hille Ris Lambers are inadequate to characterize important phylogenetic trends in character evolution in the Eulachnina; therefore, these taxa are redescribed. The evolutionary responses of morphometric traits for *Pseudessigella, Essigella* (as a whole) and two primitive *Essigella* species are deduced and interpreted with reference to Lande's models of multivariate phenotypic evolution. Twenty-six traits among these taxa were analyzed for their shape component variance using principal components analysis; ranks for the relative contribution of each trait upon the dominant two shape vectors were assigned on the basis of character loading coefficients. Between the genera, 42% of the traits were considered to be stable in their partitioned shape variance over the implied evolutionary episode; 39% of the traits showed moderate stability, while 19% were judged to be unstable. The average similarity of evolutionary response for the traits on the dominant shape vectors between these genera was 0.56; the primitive *Essigella* species showed higher similarities (0.71, 0.62) with *Pseudessigella* than did *Essigella* overall. When discriminant function analysis was used as a measure of Landean minimum selective mortality to determine the multivariately optimal traits that separate *Essigella* species, both traits with predominantly general-size variance and traits with predominantly shape variance appeared to be important in species separation. The most influential traits with the highest shape variance on the discriminant vectors, however, appeared to largely separate clades of species (i.e., species-groups or above) within the genus, rather than chiefly separating species within such groups.

Key Words.—Insecta, multivariate evolution, phylogenetic characters, natural selection, principal components analysis, discriminant function analysis

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The monotypic aphid genus *Pseudessigella* Hille Ris Lambers and its type-species, *P. brachychaeta* Hille Ris Lambers, were described from a single collection in central Asia. This interesting species represents a phylogenetic intermediate between *Eulachnus* del Guercio and *Essigella* del Guercio within the subtribe Eulachnina (Sorensen 1990), and was used as an out-group to root the phylogenetic network devised for *Essigella* (Sorensen 1987a). Because of *Pseudessigella*'s phylogenetic position, it has assumed a new importance for the study of character transformations within the Eulachnina, and for *Essigella* in particular. As a result, Hille Ris Lambers' (1966) descriptions for *Pseudessigella* and *P. brachychaeta,* although sufficient for previous taxonomic and diagnostic purposes, now fail to adequately characterize the variation, within that genus, for several traits that have been found to be important in evolution at the species and species-group levels in *Essigella* (Sorensen 1983, 1988).

This article, and Sorensen (1990), deal with the phylogenetic aspects of the Eulachnina. The latter provided an analysis of discrete, coded phylogenetic traits

and determined the phylogenetic sequence among the genera of the subtribe. This study provides analyses that indicate the multivariate evolutionary interaction of traits in both *Pseudessigella* and *Essigella,* and it serves as a base for future studies of character evolution and transformations within *Essigella* (unpublished data). The paper also redescribes *Pseudessigella* and *P. brachychaeta* in the form previously used for descriptions of *Essigella* species (Sorensen 1988), and that will also be used in a pending generic revision of *Essigella* (unpublished data).

Taxonomy

Pseudessigella Hille Ris Lambers, 1966

Pseudessigella Hille Ris Lambers 1966, Tijdschrift voor Entomologie, 109: 219.

Type Species.—*Pseudessigella brachychaeta* Hille Ris Lambers 1966, Tijdschrift voor Entomologie, 109: 219–220; by monotypy.

Redescription.—*Viviparous Apterae.* Body elongate, linear, with few hairs. Antennae five segmented, processus terminalis short. Head very slightly wider than long, unfused with pronotum. Eyes without distinct triommatidia. Rostrum retractile; last rostral segment not subdivided but short, blunt. Mesothoracic notum lightly but entirely sclerotic. Metathoracic notum mostly membranous laterally and posteriorly but with a lightly sclerotized subhemispherical shaped patch anteromesally. Abdominal dorsum with terga I–VII membranous with dorsal and marginal setae on defined sclerotic bases; tergum VIII lightly but entirely sclerotic. Siphunculi as rimmed pores on short truncated sclerotic cones, hairless, base well defined from membranous field of abdominal terga. Basitarsus with five ventral setae, lacking dorsal setae in apterae; metabasitarsus ventrally 1.5× as long as dorsally. Cauda rounded, lacking median protuberance. Profemora dorsoproximad base moderately swollen. Tarsal claws simple, not incised or bifid; tip sharp, relatively drawn out.

Other Morphs.—Unknown.

Diagnosis.—*Pseudessigella* is separated from *Eulachnus* by its five segmented antennae, and from *Essigella* by its simple unincised tarsal claws.

Pseudessigella brachychaeta Hille Ris Lambers, 1966
(Figs. 1–3)

Pseudessigella brachychaeta Hille Ris Lambers 1966. Tijdschrift voor Entomologie, 109: 219–220.

Types.—*Holotype*—viviparous aptera; data: ("WEST") PAKISTAN. Murree, 4 Jul 1964, R. van den Bosch (P-VII-4d), *Pinus griffithii* McClelland. *Paratypes*—viviparous apterae and nymphs. Holotype and paratypes slides deposited British Museum (Natural History), London, ex Hille Ris Lambers aphid collection.

Redescription.—*Viviparous Apterae. Morphology* (n = 14, measurements and counts as: range [$\bar{x} \pm$ SD]): Body length 1.950–2.505 (2.225 ± 0.206) mm. HEAD—Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim slightly greater than 0.5 × diameter of rhinarium, rhinarial membrane not conspicuously protuberant. Length of: antennal segment V 98–118 (106 ± 6) μm, processus terminalis 25–40 (34 ± 5) μm, IV 75–95 (87 ± 5) μm, III 180–220 (204 ± 11) μm, II 73–85 (79 ± 4) μm. Longest frontal setae 5–15 (12 ± 5) μm long, tips incrassate. Head width 226–390 (300 ± 46) μm. Length of: stylets 475–542 (509 ± 24) μm, ultimate rostral segment 70–93 (74 ± 6) μm; rostral tip reaching slightly past mesocoxae. Head and pronotum not fused, their combined length 390–447 (422 ± 21) μm. THORAX—Length of: mesothorax 304–371 (331 ± 17) μm, metathorax 63–93 (76 ± 10) μm. Meso-, metathorax and abdominal segment I not fused. ABDOMEN—Maximum distal width of flange on

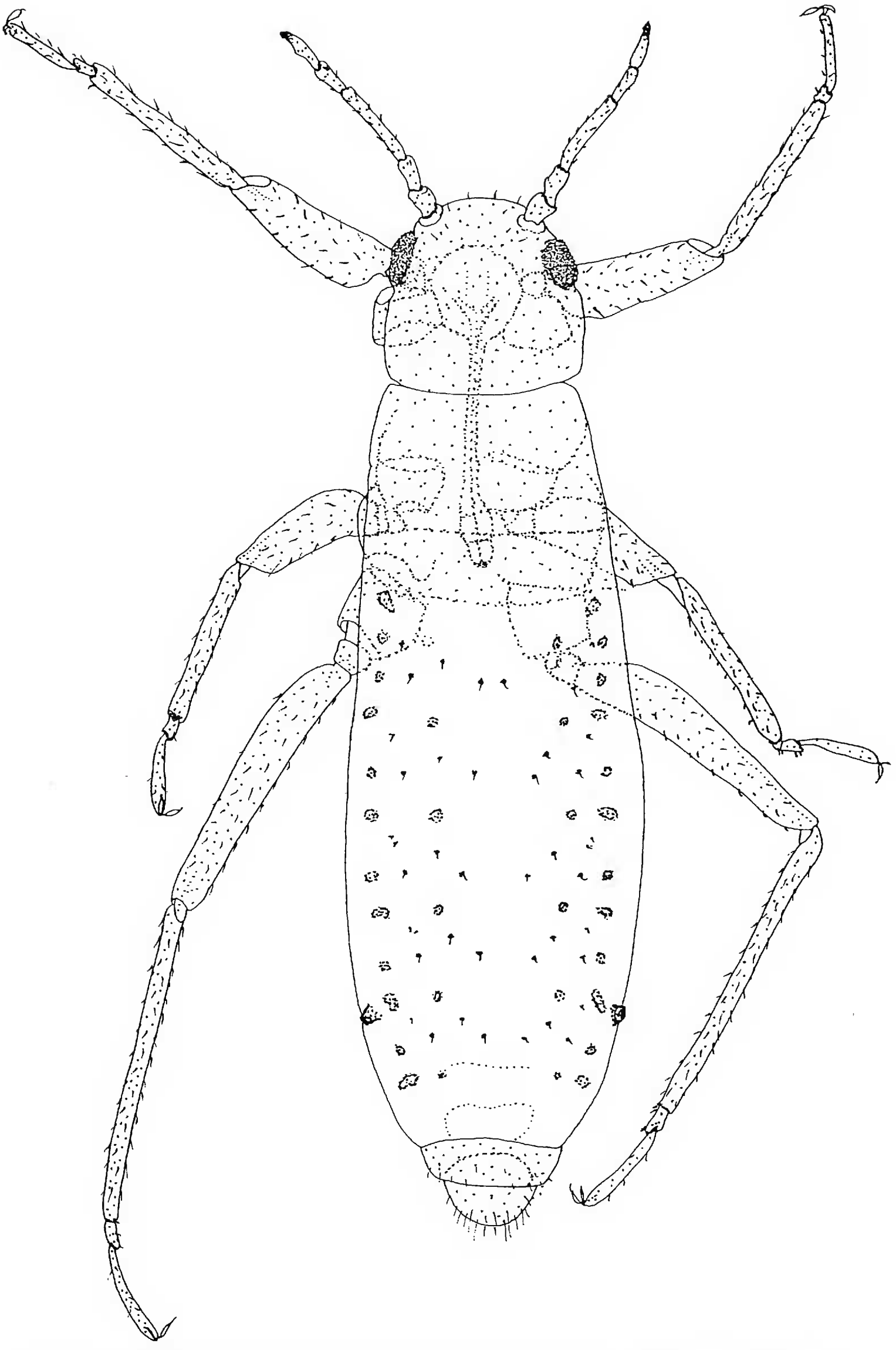


Figure 1. *Pseudessigella brachychaeta* Hille Ris Lambers. Body setae omitted except frontals and setal positions on dorsum of abdomen. Sclerotic areas stippled.

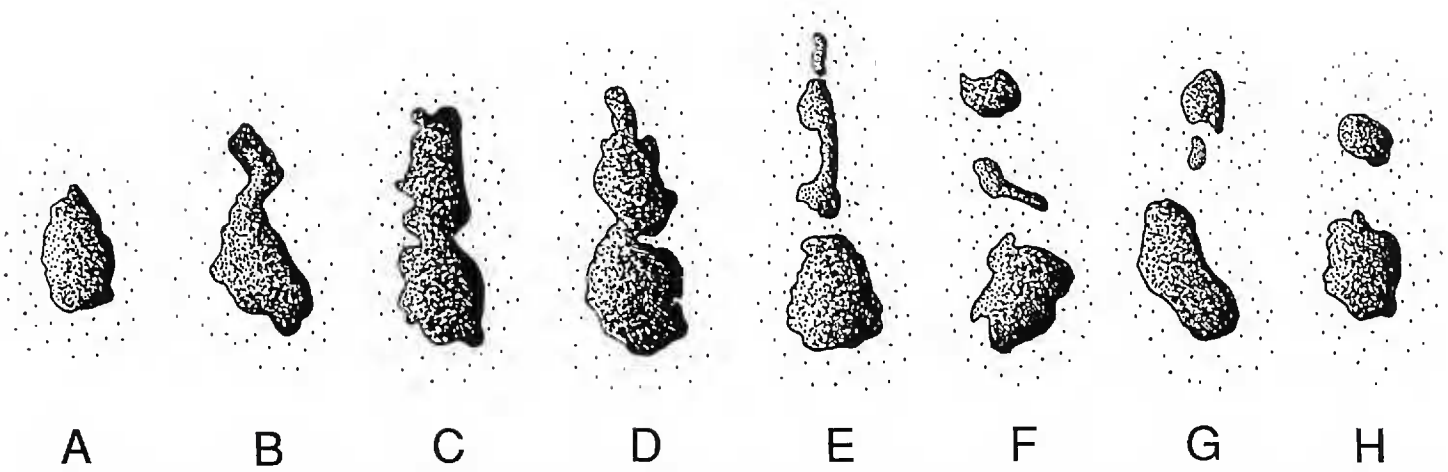


Figure 2. Expression of ventral abdominal sclerites on abdominal segments II–IV in *Pseudessigella.* The sclerites, which serve as muscle attachment points, vary from a single, subelliptical to linear sclerite (A–D), often with constrictions (B–D), to a bipartite (H) or tripartite (E–G) series of sclerites, in which the anterior (E) or usually the central (F, G) sclerite is diminished. (Shading indicates sclerotization; no transformation is implied.)

siphunculi 23–28 (24 ± 2) μm; siphunculi truncated sclerotic cones, protruding to 0.5 × maximal distal width. Ventral abdominal sclerite shape on segments II–IV (Fig. 2) variable, often linear with posterior enlarged but anterior narrow, sometimes broken into two to several minor plates: the posterior then subquadrate, subcircular to subelliptical and the anterior plate(s) smaller, more irregular, size 0.2–0.5 × posterior plate and more variable in shape from subquadrate, subcircular or subelliptical to asterisk-like, mere specks or absent; entire linear sclerite (or series of broken platelets) 35–95 (63 ± 19) μm long, 1.0–2.0 × metatibial diameter. Dorsal setae on abdominal terga II–IV (Fig. 3) dividable into major and minor series; six major dorsal setae across medial portion of tergum of each abdominal segment, arranged in roughly transverse irregular, meandering or staggered row, positions (if numbered left to right) of setae number 1, 3, 4 and 6 nearly in straight row, but setae number 2 and 5 slightly to moderately anterior of that row, on relatively larger (12–15 μm diameter) scleroites (sclerotized platelets at setal bases), with incrassate tips; minor dorsal setae on relatively smaller scleroites (8–10 μm diameter), like marginal setae but present mesally between lateral most dorsal abdominal muscle

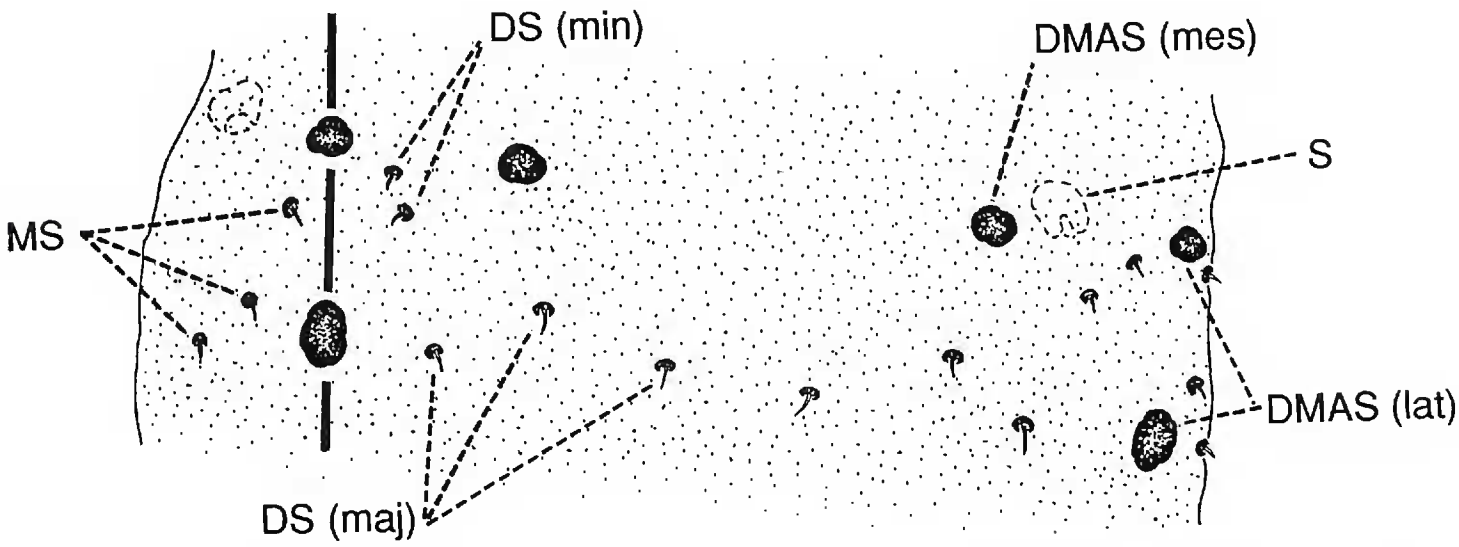


Figure 3. Setal positions on dorsum of abdominal terga II–IV in *Pseudessigella.* The abdominal segment shown is slightly skewed to the right showing more of its left lateral face; items are indicated on one side only. Dorsal muscle attachment sclerites occur as three sclerites on each side of the segment and are represented by a single mesad sclerite, DMAS (mes), and a pair of laterad sclerites, DMAS (lat); the dark bar oriented through the laterad sclerites on the left indicates the "territorial" line that is used here to separate (define) the minor dorsal versus marginal setae. Dorsal setae occur in two series, a transversely oriented and staggered set of six major setae, DS (maj), which cross the center of the segment, and a cluster of no to four minor setae, DS (min), on each side of the segment just mesad to the lateral dorsal muscle attachment sclerites. Marginal setae, MS, occur as a set of two to six setae laterad of all dorsal muscle attachment sclerites. Spiracles, S, that occur ventrally may be confused with other sclerites in slide preparations.

attachment plates and slightly mesad to them, all tips incrassate, arranged in loose cluster(s) anterolaterally and also sometimes posterolateral of major dorsals, each side with 0–4 (1.7 ± 0.8) component setae. Marginal setae (lateral to lateral most dorsal abdominal muscle attachment plates) with incrassate tips, on small scleroites (8–10 μm diameter), 4–12 per segment, each side with 2–6 (4.6 ± 0.6), apparently arranged in two to four subgroupings. Abdominal tergum VIII with 10–16 (14.3 ± 1.8) hairs, 10–15 (11 ± 2) μm long, tips incrassate, subregularly placed. Cauda rounded, caudal protuberance absent, longest caudal setae 40–80 (67 ± 10) μm long, tips sharp. LEGS—Length of: metafemora 561–646 (624 ± 30) μm, metatibiae 637–741 (700 ± 30) μm; longest dorsal setae on central one-third of metatibiae 8–18 (12 ± 3) μm long, 0.1–0.5 × metatibial diameter, tips incrassate, approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae 23–30 (27 ± 3) μm long, tips sharp. Length of: metabasitarsus 50–88 (69 ± 9) μm, metadistitarsus: 225–255 (243 ± 8) μm. Ratio of metabasitarsus to metadistitarsus averaging 1.0:3.6, ranging from 1.0:2.8 to nearly 1:5. *Pigmentation.* Color in life pale green (Hille Ris Lambers 1966). Prepared specimens: background of sclerotic body dorsum pale (to approximately 40% pigment density [as solid black in a 54 line/cm screen]), unicolorous. Frontal setal bases concolorous with surrounding terga, undifferentiated. Thoracic muscle attachment plates dusky, inconspicuous to conspicuous. Dorsal and marginal setal bases on abdomen dark, conspicuous, arising from distinct scleroites that contrast the membranous abdominal field. Dorsal muscle attachment plates of abdomen, spiracular plates, siphuncular cones and ventral abdominal sclerites pale, usually dusky light brown (to 60% pigment density), conspicuous. Cauda, anal and subgenital plates concolorous, slightly less dark than head and mesothorax. Antennal segments V and IV slightly to moderately dusky over entire segment, to moderately brown distally, III pale to moderately dusky distally, II concolorous with proximad section of III and I concolorous with frons. Pro-, meso- and metatibiae dusky, concolorous, slightly more dusky than remaining sclerotic body dorsum.

Ultimate Stadium Nymphs of Viviparous Apterae.—Nonmorphometrics and pigmentation of prepared specimens as described for viviparous apterae.

Viviparous Alatae, Males, Oviparae, Fundatrices.—Unknown.

Diagnosis.—*Pseudessigella brachychaeta* is the only species in the genus, and the only known linear-bodied aphid feeding on the needles of Pinaceae which has both a five segmented antennae in adults and simple, unincised tarsal claws.

Host.—*Pinus griffithii* McClelland, stated to be "*Pinus excelsa*" on the type series slides and "*Pinus wallichiana* (*excelsa*)" in the original description (Hille Ris Lambers 1966). *Pinus wallichiana* A. B. Jacks and *Pinus excelsa* Wallich ex Lambert are synonyms of *P. griffithii* (Critchfield & Little 1966, Mirov 1967, Little & Critchfield 1969).

Range.—Known from one collection in ("West") Pakistan at Murree. Potential native range (see discussion), assumed to be the distribution of *P. griffithii* (Fig. 4), is throughout Himalaya Mountains to eastern Afghanistan, northeastern Burma and Yunnan Province, China (Troup 1921, Vavilov 1959, Critchfield & Little 1966, Mirov 1967); in mid- and high elevation forests, especially in drier inner valleys (Critchfield & Little 1966). Neither the collection sample nor description quote an elevation, but Hille Ris Lambers (1966) described several other new aphid species, also taken by van den Bosch in a sequence of field collections at Murree between 30 Jun–5 Jul 1966, and cited elevations of 2132–2284 m (7000–7500 ft) for those collections. These elevations agree with Mirov's (1967) notation that in the "Murree Hills, Rawalpindi," *P. griffithii* grows from 1200 m (in cool, moist conditions) to above 2000 m, where it occurs in pure stands or mixed with broad-leaf trees.

Etymology.—The species was named for its short setae.

Discussion.—*Pseudessigella* is phylogenetically intermediate between *Eulachnus* and *Essigella,* the more ancestral and derived genera respectively, of the subtribe Eulachnina (Sorensen 1990). *Pseudessigella,* like *Eulachnus,* appears to be

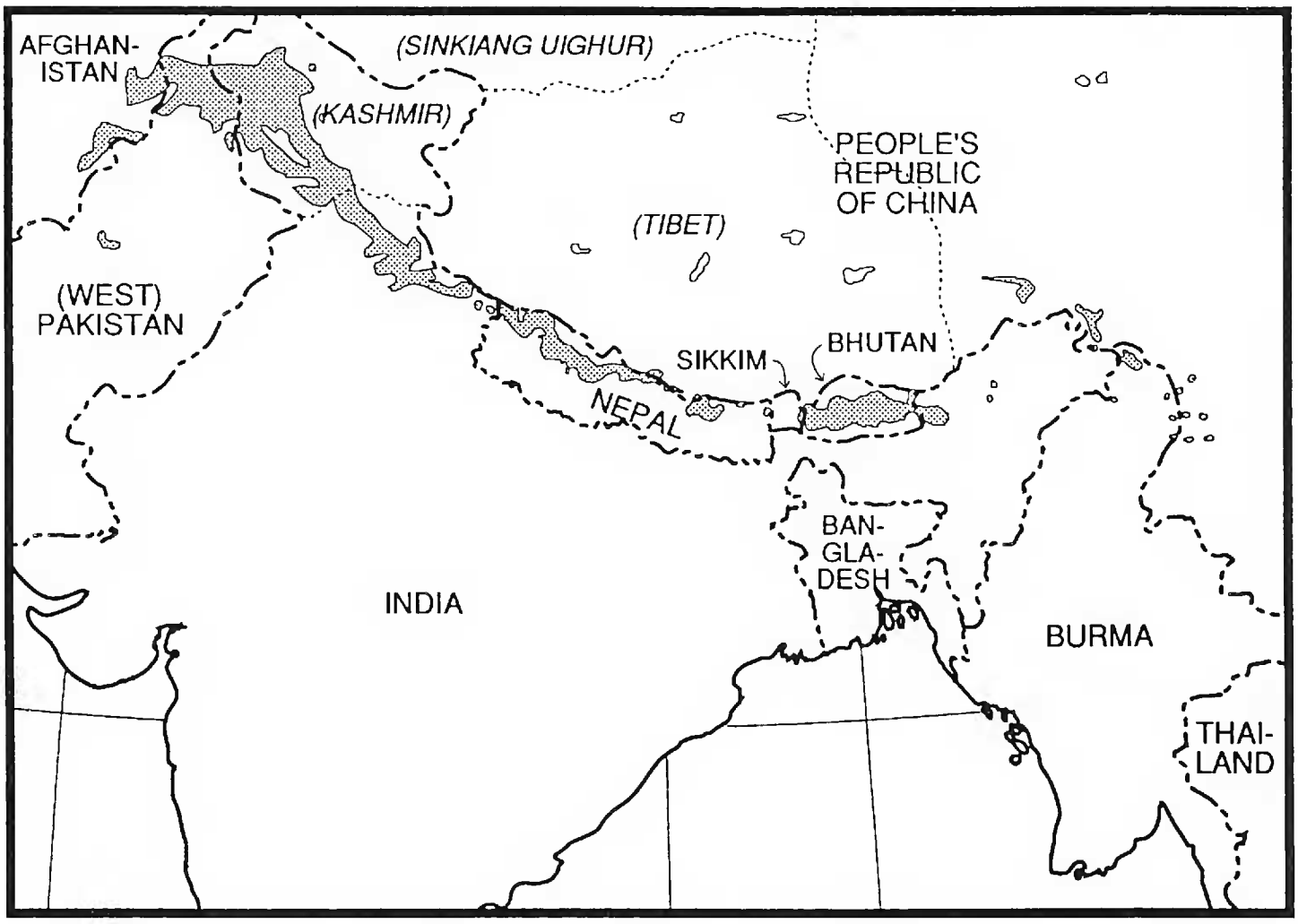


Figure 4. Potential range of *Pseudessigella brachychaeta* (= distribution of *Pinus griffithii* [Critchfield & Little 1966]).

paraphyletically defined; although monotypic, *Pseudessigella* lacks a unique defining autapomorphy. *Pseudessigella* shares with *Essigella* the following apomorphic character states: differentiation in size, shape, tip condition or projection angle of dorsal versus ventral setae on antennal segments and tibiae (partially shared with *Eulachnus*); absence of secondary rhinaria on ultimate and penultimate antennal segments (a homoplasy with *Schizolachnus*); a reduction of antennal segments to five in adults; and representation of abdominal tergum VIII as a single, entire sclerotized field not apparently formed from fused lateral sclerites associated with dorsal setal bases (see Sorensen 1990). *Pseudessigella* resembles *Eulachnus* in having the following symplesiomorphies: unincised tarsal claws, a membranous abdominal dorsum, and a head separated from the pronotum in adult viviparous apterae.

Slide mounted adult viviparous apterae of *Pseudessigella* are somewhat superficially similar to late stadium nymphs of the apterae of *Essigella,* especially the most plesiomorphic species (e.g., "group I" of Sorensen [1987a]: *E. kathleenae* Sorensen and *E. kirki* Sorensen, although usually darker than both) or slightly more derived species (e.g., "group II" of Sorensen [1987a]: *E. fusca* Gillette & Palmer and its relatives). Adult *Pseudessigella* differ most noticeably from the nymphs of any *Essigella* species (other than in adult genitalic traits) by their elongated metabasitarsus to distitarsus ratio; averaging 1.0:3.6 for *Pseudessigella* versus slightly over 1.0:2.05 for *E. kathleenae,* the longest among *Essigella.* This "long distitarsus" ratio probably represents a relative plesiomorphy for *Pseudessigella* (see discussion of analyses below) within the Eulachnina, despite impli-

cations of Mamontova (1972) to the contrary for the Cinarini, and is more similar to conditions in *Cinara* and *Schizolachnus.*

The tarsal trait is homoplasious among the Cinarini, including the Eulachnina (Sorensen 1990). In contrast to *Pseudessigella, Eulachnus* and *Essigella* appear to have homoplasiously evolved an apomorphically shorted metatarsal ratio among species-groups occupying differing niches in varying pine groups (unpublished data). In at least the case of *Essigella* this may possibly represent a "resource-tracking" attribute (sensu Brooks 1981, see Moran 1986). A more detailed discussion of the relationship of *Pseudessigella* within the Eulachnina is dealt with in Sorensen (1990), which comments more fully upon character states thought to be of phylogenetic significance for the genus and discusses Mamontova's (1972) contrasting phylogenetic concepts and character transformations, considered erroneous in part, for the eulachnine aphids.

The phylogenetic relationships among (Sorensen 1990), and biological associations within (Sorensen 1987a), the eulachnine genera make ecological predictions possible for *Pseudessigella* allowing future corroboration. Among the Eulachnina, *Pseudessigella* and *Eulachnus* are Palaearctic, although the latter has been introduced into the Nearctic where it apparently feeds chiefly on cultivated old world pines; I have taken *Eulachnus* only on Palaearctic species of cultivated *Pinus* in the western Nearctic (unpublished data), despite intensive collecting for *Essigella* on natural and planted stands of native Nearctic pines (Sorensen 1983). *Essigella* is Nearctic and shows phylogenetic associations among *Pinus,* but dissident derived species (in "group III," Sorensen [1987a]) also feed upon *Pseudotsuga* and *Picea.* Because nothing is known of the biology of *P. brachychaeta,* except that the single collection of it in the Himalayas was on *Pinus griffithii,* biological predictions for *Pseudessigella* must be based on *Eulachnus* and especially *Essigella,* particularly "groups I and II" (Sorensen 1987a).

Based upon biological knowledge of "group I" *Essigella* (Sorensen 1983, 1987a, 1988, unpublished data), I suspect that *P. brachychaeta* shares the rather monophagous feeding habits of *E. kathleenae* and *E. kirki.* It, therefore, seems reasonable that the range of *Pinus griffithii* itself (Fig. 4) should be a probable indicator of the potential native distribution of *P. brachychaeta,* as has been found in these group I *Essigella.* The host of *P. brachychaeta, Pinus griffithii,* is a haploxylon pine in the section Strobus, subsection Strobi of *Pinus* (*Strobus*) (Little & Critchfield 1969). Subsection Strobi also contains the hosts of these two most primitive *Essigella*: *Pinus lambertiana* Douglas for *E. kathleenae,* and *Pinus flexilis* James and *P. strobiformis* Engelmann (a slightly overlapping allopatric species previously considered a variation [*reflexa* Engelmann] of *flexilis* [Critchfield & Little 1966: 7, map 8]) for *E. kirki* (Sorensen 1987a, 1988).

Species of *Essigella* and *Eulachnus* are fast moving when disturbed, and relatively solitary; these behavioral traits are assumed to be typical of *Pseudessigella* also. I suspect the (now unknown) alatae of *Pseudessigella* are (will be found to be) relatively uncommon, because alatae of *E. kathleenae* and *E. kirki* remain unknown despite extensive sampling (Sorensen 1983), although alatae of more derived *Essigella* groups, particularly some group III representatives (e.g., *E. californica* (Essig) and *E. hoerneri* Gillette & Palmer) can be quite common.

In previous phylogenetic studies on *Essigella,* I have referred to *P. brachychaeta* using the acronym "PLES" (Sorensen 1983) and "Sp. X" (Sorensen 1987a). In

the latter study, which used a maximum-likelihood algorithm (Felsenstein 1984) to construct a phylogenetic network based upon centroid values on discriminant functions, *E. kirki* (Sorensen 1987a: sp. K) was considered to be the most plesiomorphic *Essigella* species because it showed the shortest distance on the phylogenetic pathway to *Pseudessigella*; *E. kathleenae* (Sorensen 1987a: sp. J) was slightly more "advanced" on that network. This study, however, provides evidence that *E. kathleenae,* rather than *E. kirki,* displays several attributes that may be more plesiomorphic in their similarity to those of *Pseudessigella*: (a) *P. griffithii,* the host of *Pseudessigella,* is genetically close enough to be one of the few pines that hybridizes with the *Pinus lambertiana* (Sorensen 1987a; W. B. Critchfield, personal communication), the host of *Essigella kathleenae*: (b) *E. kathleenae* displays the relatively highest (more plesiomorphic) ratio of the metadistitarsus to metabasitarsus within *Essigella* (Sorensen 1988); and (c), perhaps most convincing, *E. kathleenae,* rather than *E. kirki,* shows a higher similarity value for shape component variance with *Pseudessigella* (see multivariate evolution section).

Material Examined.—The type-series viviparous apterae and nymphs have been examined, and represent the only known specimens.

Multivariate Evolutionary Responses for Characters

In any organism, continuous phenotypic variation is caused by genetically correlated characters that are linked by many covarying genes (Lande 1980). The evolutionary aspects of such correlated traits are assumed to be predominantly under the genetic influence (Falconer 1981). Each gene has a relatively minor influence in the evolutionary change of either the overall phenotype or any particular phenotypic attribute, because these changes are due to an integrated, additive genetic effect, plus minor additive environmental influences (Lande 1985, 1988). The evolution of species and character interactions under such quantitative genetic systems is based upon an (admittedly simplistic) phenotypic model for the multivariate evolution of correlated morphological character suites developed by Lande (1979). This model has been employed previously to determine the phylogenetic relationships among aphids (Sorensen 1983, 1987a) and birds (Schluter 1984), as well as phenological shifts in phenotype between sibling species of leafhoppers (Sorensen 1987b, Sorensen & Sawyer 1989).

Lande's model allows reconstruction of the net gradients of genetic selection (taken as phenotypic responses where the environmental component is effectively null) within and between groups with approximately equal genetic covariance matrices. The model permits an estimation of the degree to which net selective pressures have acted upon characters within suites of correlated phenotypic traits during evolution. Under this multivariate model of evolution the traits respond to given historical net selection gradients, to drive the mean group phenotype for a species or population through the dimensional multivariate evolutionary space defined by all such gradients.

For a given individual's phenotype, a single trait, z_i, contributes to the evolution of that phenotype and thus itself evolves in relation to other traits, z_j, as (Lande 1979: equation 7b):

$$\Delta \bar{z}_i = \sum_{j=1}^{m} G_{ij} \partial \ln \bar{W} / \partial \bar{z}_j$$

where minor selective change on trait z_i is the sole cause of differences in Malthusian mean fitness ($\partial \ln \bar{W}/\partial \bar{z}_j$); and z_i shows no correlated effects, whereas other traits, z_j, are constant with $j \neq i$ (Lande 1979). Therefore, over each generation, changes in the trait z_i include genetic gains from selection that act upon both it and z_j, as other genetically correlated characters. The measurement of selection on correlated traits is discussed in more detail by Lande & Arnold (1983).

Principal components analysis (PCA) is particularly suited as a practical, analytical probe to determine the multivariate evolutionary responses of characters in covarient suites as they react in unison to historically imposed selection regimes (Sorensen 1987a, b; Sorensen & Sawyer 1989). In a usual (Q-type) PCA, each eigenvector represents a historical net natural selection gradient (as: $\nabla \ln \bar{W}$, sensu Lande 1979) in multivariate evolution; the mean group phenotype of a species evolves along these gradients (eigenvectors) due to the concert action between its genetic covariance matrix and the vector as a selection regime. The relative input weight of each character on any given eigenvector shows the relative amount of its partitioned and sequestered variance that can be attributed to the covariant character suite that is defined by that vector (Sorensen 1987b, Sorensen & Sawyer 1989).

During multivariate evolution, the characters in any such covariant suite of traits respond to the net evolutionary selective pressures of their eigenvector in an integrated fashion, according to the relative degree and sign of their vector loading coefficients. All traits belong in varying degrees to all covariant character suites, with each suite responding to a particular vector's selection gradient; this is because the traits each have a contributing (weighted) input on each eigenvector which varies among the vectors.

During evolutionary response to selection pressures, each covariant suite of traits is driven chiefly by dominating traits ("drivers") which are those characters with the highest absolute loading coefficients (and correlations) on the given vector. In contrast, traits with near zero loading coefficients on any vector are more subordinate for that suite and accordingly more neutral in response to the net selection pressures defined by that eigenvector as an evolutionary selection gradient. Therefore, when selection is imposed upon any suite, it acts largely upon the dominating "driver" traits but causes modification of all traits in proportion to their loading input and correlation for the given vector.

Although stabilizing selection maintains linkages, and thus integrated reaction to selection, among the traits in each character suite, if enough disruptive selection force is applied to a given trait in a suite it may cause the "shearing" of that trait from the suite. The remaining traits in the suite would be initially modified also by the disruptive selection, along with the trait to which it was applied, but they would eventually "break-away" as an integrated unit and return to their former expression values leaving the disrupted strait to evolve separately from the suite. Zeng (1988) discusses the complicating effects of stabilizing and disruptive selection upon characters in multivariate evolution.

Character interaction during multivariate evolution can be examined using an R-type analysis in PCA. In an R-type analysis, each of the individuals, rather than the attributes (as in Q-type PCA), provides the input coefficient along the orthogonal eigenvectors, and the positions of the original characters are plotted along these vectors in the I-space defined by the values derived from individuals

(Williams & Dale 1965, Sneath & Sokal 1973). An R-type analysis thus depicts spatially the relative degree of association and interaction between each trait along orthogonal eigenvectors as character, rather than populational, responsive models of Landean gradients of net natural selection.

R-type PCA also allows a perspective dependant portrayal of the relative integrated response of functional (virtual) groups of characters to several independent selection gradients (as orthogonal eigenvectors). Such functional groups of characters may show an orchestrated response to simultaneously imposed multiple selection regimes during multivariate evolution. These virtual groups of characters are recognizable by their relative spatial affiliations when more than one R-type eigenvector is plotted; the apparent groups of characters may react relatively similarly to the equally induced selection pressures on the vectors. Such virtual character groups defined by multiple vector plots may exist over any partial subsets of the summarized n-1 eigenvectors.

Because of its usefulness as an analytical probe, R-type PCA was used here to determine the historical interaction of characters among the taxa during the multivariate evolution of the eulachnine aphids.

Methods

Determination of "Shape" as a Character Component.—To determine the relative influence and stability of shape component variance among traits during the multivariate evolutionary episode between *Pseudessigella* and *Essigella,* and within group I (Sorensen 1987a) of *Essigella,* data were analyzed for all taxa and compared. Although many controversial criteria and experimental methods have been advanced to completely partition multivariate "shape" from "size" in data matrices (e.g., Burnaby 1966; Bookstein 1986, 1989; Bookstein et al. 1985; Humphries et al. 1981; Rohlf & Bookstein 1987; Somers 1986, 1989; Sundberg 1989) none have been completely successful, and all adulterate the generated evolutionary space by various methods, such as shearing. To avoid the philosophical problems inherent in such methods, especially with reference to existing models of multivariate evolution, it was decided to represent "shape" here as simply principal component vectors 2-n, with vector 1 taken as (chiefly) a size factor if there appeared to be high loadings and correlations for traits such as segmental body lengths, which normally are overtly general-size dependant.

Material and Data Examined.—Analysis of *Pseudessigella brachychaeta* employed the paratype adult viviparous apterae (n = 14), which represent the only known collection (see taxonomy: material examined). Analyses of *Essigella* used exemplars of adult viviparous apterae that represented the nonclonal, intraspecific variance shown within *E. kathleenae* (n = 13, morphometric data in Sorensen [1983: appendix E1, "KATH"]), *E. kirki* (n = 12, morphometric data in Sorenson [1983: appendix E1, "HOTT"]), and all *Essigella* species (n = 255, morphometric data in Sorensen [1983: appendix E1, all acronyms excluding "PLES"]); hereafter, the use of "*Essigella*" refers to the collective concept of its pan-generic variance, including that shown by *E. kathleenae* and *E. kirki.* Locality data for examined material of *E. kathleenae* and *E. kirki* is listed in Sorensen (1988); it is available for all examined material of *Essigella* in Sorensen (1983) by cross-checking the collection numbers in appendix E1 with locations in appendix A1.

All specimens were measured from the slide mounted material, employing the

Table 1. Morphometric characters.

Number	Acronym[a]	Character descriptions
1	LBODY	length of body, vertex to posterior of abdominal segment VIII excluding cauda.
2	LANT5	length of total antennal segment V.
3	LANT5PT	length of processus terminalis, proximal rim of accessory rhinaria to tip.
4	LANT4	length of antennal segment IV.
5	LANT3	length of antennal segment III.
6	LANT2	length of antennal segment II.
7	LHFRON	length of longest seta on the frons.
8	WOANT	(body) width taken at lateral most (outer) portion of the rim of the antennal sockets.
9	LSTY	length of the stylets.
10	LUROST	length of the ultimate rostral segment.
11	LHEAD	combined length of the unfused head plus pronotum, along the median dorsal body axis.
12	L2THOR	length of the mesothoracic notum, along the median dorsal body axis.
13	L3THOR	length of the metathoracic notum, represented as a sclerotic plate in the otherwise membranous metathoracic field, along the median dorsal body axis.
14	WSIPH	maximal distal width of the siphuncular flange.
15	LVABSC	maximum length of the longest ventral abdominal muscle attachment sclerite(s) on abdominal segments II-IV (combined length in the case of bi- or multi-partite subsclerites in quasilinear array).
16	NHAB2DT	maximum total number of combined major and minor dorsal setae (between dorsal muscle attachment sites) on abdominal terga II–IV.
17	NHAB2M	maximum number of marginal setae (lateral to dorsal muscle attachment sites) on abdominal terga II–IV.
18	NHAB8	number of setae on abdominal tergum VIII.
19	LHAB8	length of longest seta on abdominal tergum VIII.
20	LHCAUD	length of longest seta on cauda.
21	L3FEM	length of metafemur.
22	L3TIB	length of metatibia.
23	LH3TIBD	length of longest seta along the central one-third of the dorsal surface of the metatibia.
24	LH3TIBV	length of longest seta along the central one-third of the ventral surface of the metatibia.
25	L3TAR1	length of the metabasitarsus.
26	L3TAR2	length of the metadistitarsus.

[a] Acronym for trait used in Sorensen (1983).

26 traits (Table 1) used previously for *Essigella* (Sorensen 1983, 1987a, 1988). Measurements were done with a Zeiss compound microscope using an ocular scale at up to 400×, and are assumed accurate to 2 μm for the smallest structures observed. The data for *Pseudessigella, E. kathleenae* and *E. kirki* were log-transformed to minimize the influence of scaling. The data for *Essigella,* however, were not log-transformed; analyses of log-transformed versus nonlog-transformed data for sequestered parts of that matrix suggested that the obtained vector loading coefficients did not appear to differ significantly.

Algorithms and Analyses.—All data were subjected to an R-type principal component analysis. Analyses for *Pseudessigella, E. kathleenae* and *E. kirki* were conducted on a Macintosh® computer and used Statview512+® (BrainPower, Inc., Calabasas, California). Analyses for *Essigella* were conducted on a CDC6400 computer using the algorithm "PNCOMP" (Duncan & Phillips 1980); analytical checks of smaller subsections of the *Essigella* data indicated that the output for PNCOMP was equivalent to that of Statview512+, as used for the other data. All PCA solutions yielded unrotated, orthogonal vectors, and the derived loading coefficients for the characters were used to portray each trait's influence on the vectors. To determine the multivariate diagnostic value of characters for separating all species within *Essigella,* that matrix underwent discriminant function analysis (SPSS version 7 subprogram "DISCRIMINANT," direct selection, Wilks-λ criterion; Klecka [1975]).

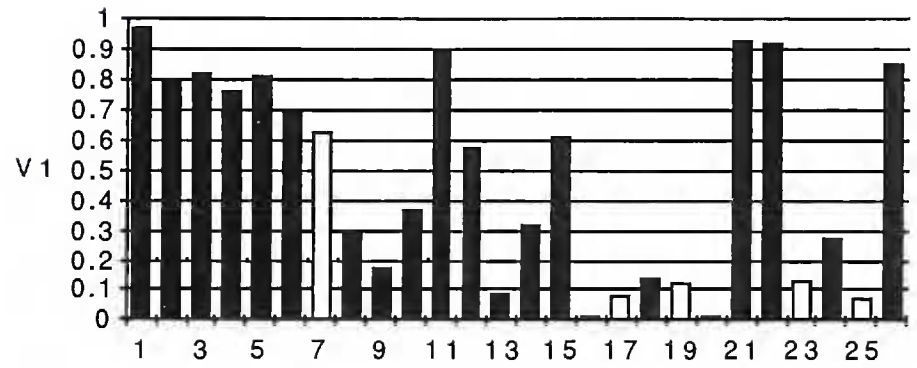
Results of the analysis on *Pseudessigella* are presented using histogram illustrations of the loading coefficients were created with Excel® (Microsoft Corporation, Redmond, Washington). For *Pseudessigella,* the virtual groupings of characters that occur in the evolutionary space defined by multiple vectors, were assessed by transferring the vector loading coefficients derived from the unrotated factor matrix to MacSpin® (D^2 Software, Austin, Texas), a three-dimensional X-Y-Z coordinate rotation program on the Macintosh; scattergrams composed of orthogonal combinations of multiple vectors were then rotated to assess the potential groupings of characters in the differing rotational perspectives.

To determine the relative importance of each trait upon any generated eigenvector, the vector loading coefficients of the traits were grouped and ranked into three classes. This was done by dividing the scale between the highest and lowest absolute (sign-less) vector loading coefficients for a given vector into equal sized class partitions, and then assigning each trait to its appropriate class, based upon its loading coefficient for the vector. The values of shape influence for traits were determined for all taxa by assigning to each trait its greatest ranking on either vectors 2 or 3 of the PCA (as the dominant shape vectors) for the taxa. The ranking of traits as multivariate separators within *Essigella* was similar, except that discriminant vectors 1–3 were ranked.

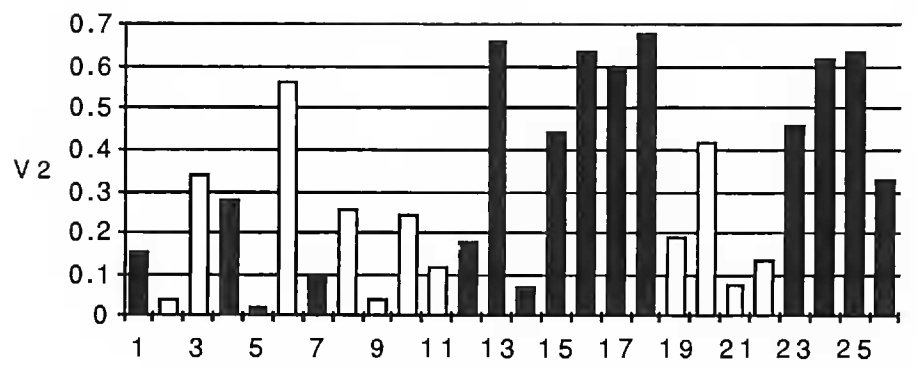
Shape Stability between Taxa.—The evolutionary stability of shape components between pairs of taxa was calculated as intertaxon similarities. These were determined by assigning a distance value of 0.5 to any one-rank-step change for a character between two taxa; a value of 1.0 was assigned for any two-ránk-step change. The summed total distance between any given taxon-pair was then divided by 26, which represented the total potential distance for changes among all characters. The derived distance fraction was converted to a similarity fraction by subtracting it from 1.0, which represented absolute similarity.

Results and Discussion

Histograms in Figs. 5 and 6 depict the relative contributions of the traits for *Pseudessigella,* among the character suites defined by vectors 1–6. In those figures, the trait contributions for each suite are represented as the absolute values for loading coefficients of the traits on vectors 1–3 (Figs. 5A–C) and 4–6 (Figs. 6A–C). Despite the log-transformation conducted on the data, vector 1 (Fig. 5A) seems to retain a quite high affiliation as a general-size component. The relative influence



A



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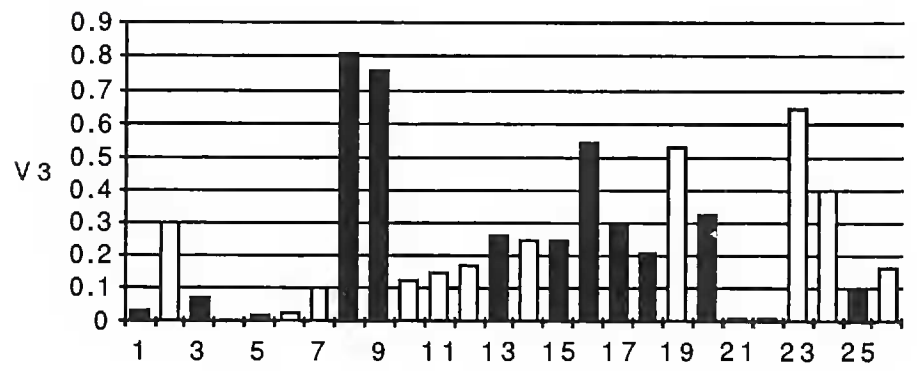

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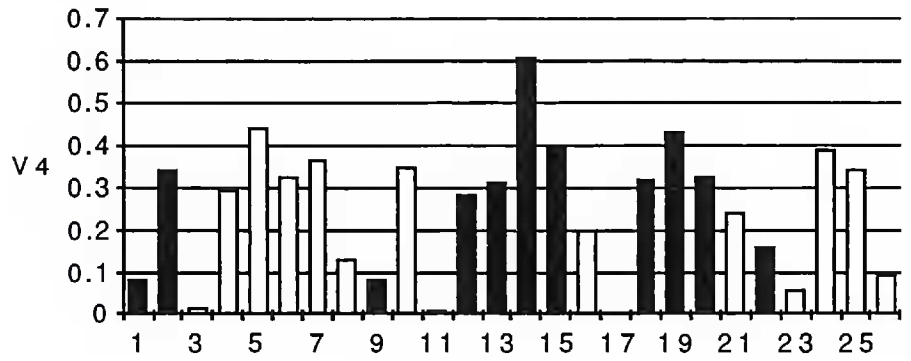
Figure 5. Histograms indicating each trait's relative influence in covariant character suites. Each suite is represented as an orthogonal PCA vector upon which the trait responds in proportion to its vector loading coefficient value; a black bar indicates positively loading traits, a white bar indicates negatively loading traits. (A) vector 1, (B) vector 2, (C) vector 3.

of allometric size versus shape, as separable components of total variance, is illustrated in Fig. 7A, which compares the percentage of summed absolute vector loading coefficients for the traits on vector 1 (Fig. 7A: white), as a size component, versus vectors 2–6 (Fig. 7A: black), as shape components. The relative contribution of each trait to size or shape variance is also shown in Fig. 7B, where all influences have been scaled to 100% rather than represented as the summation of vector loading coefficients, as in Fig. 7A. In Fig. 7B the contribution of general size to each trait is shown in white, while its shape contributions are in nonwhite; shape contributions on vectors 2 and 3 (the two most dominant shape vectors) are in gray, and those of vectors 4–6 are in black. An approximation of "uniqueness," or differentiation, among the traits is depicted in Fig. 7C, as variance not due to common factors in the sense of pleiotropy. A spatial portrayal of character groupings based upon the dominant three shape factors, vectors 2–4, is shown for *Pseudessigella* in Figs. 8A–B. Figure 9 depicts, in tabular form, the rankings of shape variance across all taxa, and the diagnostic value of traits for group



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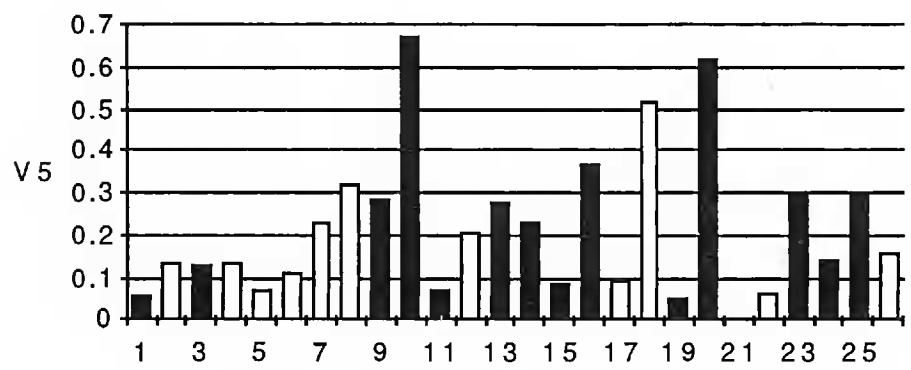

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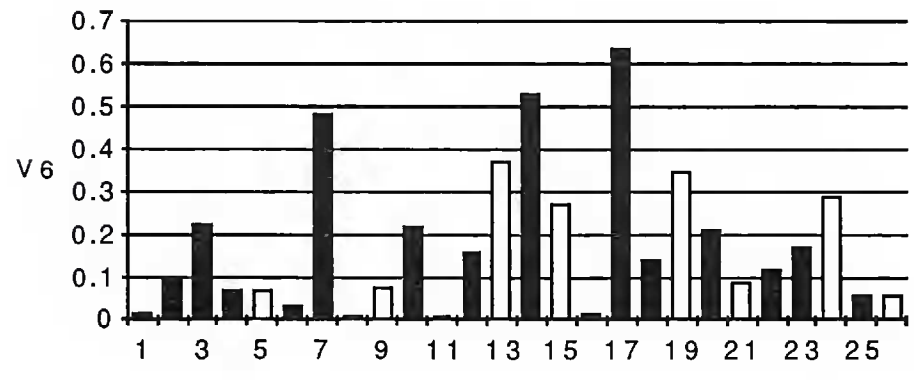

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Figure 6. Histograms indicating each trait's relative influence in covariant character suites. Each suite is represented as an orthogonal PCA vector upon which the trait responds in proportion to its vector loading coefficient value; a black bar indicates positively loading traits, a white bar indicates negatively loading traits. (A) vector 4, (B) vector 5, (C) vector 6.

separation within *Essigella.* Figure 10 shows the relative similarity in shape component stability of the taxa analyzed.

Multivariate Character Suites within Pseudessigella.—The dominant six vectors derived from the *Pseudessigella* matrix accounted for 84.0% of the total variance (34.1, 15.2, 11.8, 8.9, 7.7 and 6.3%, respectively for vectors 1–6), indicating that character variation within *Pseudessigella* is reasonably complex, as found for various species-groups within *Essigella* (Sorensen 1983).

Vector 1 (Fig. 5A) is interpretable as a size factor because most body appendage lengths (characters 1–6, 11, 15, 21, 22 and 26) load and correlate highly and positively upon it. Only those traits poorly related or unrelated to size were not influential on vector 1. Notable exceptions are those traits (13 and 25 as lengths for the metathoracic nota and the metabasitarsus) which might have been expected to load more strongly with general-size; trait 7 (frons setal length) loads highly but negative; traits 8, 9, 13, 14, 16–20, and 23–25 show relatively minor and often negative relations with general-size.

Vector 2 (Fig. 5B) represents a covariant suite driven largely and positively by traits 13, 16–18, 24 and 25, and to a lessor extent by traits 15 and 23; the suite is driven negatively by trait 7 and less so by trait 20. This suite involves the metathoracic nota, the ventral abdominal sclerites, the number of setae on abdominal segments, the metatibial setae and the metabasitarsus, all of which interact negatively with the length of the frons setae. The character suite shown by vector 3 (Fig. 5C) is driven positively by traits 8 and 9, and less so by trait 16; it is driven most negatively by traits 19 and 23. Vector 3 involves body width, stylet length and the number of dorsal setae on the abdomen, all of which interact negatively with the length of setae on abdominal tergum VIII and the length of the dorsal setae on the metatibiae. The suite for vector 4 (Fig. 6A) is more complex, with several traits giving a moderate interactive influence; the suite is driven most strongly, however, by trait 14, a siphuncular width function. The suite for vector 5 (Fig. 6B) is dominated positively by traits 10 and 20, and negatively by trait 18. It involves the lengths of the ultimate rostral segment and the caudal setae, which interact antagonistically with the number of setae on abdominal tergum VIII. The suite for vector 6 (Fig. 6C) is driven positively by traits 7, 14, and 17, with traits 13 and 19 reacting negatively and less strongly. The setae on the frons, the width of the siphunculi and the number of marginal setae on the abdominal segments react positively in this suite, while the metathoracic notum and the length of setae on abdominal tergum VIII react negatively.

For this *Pseudessigella* matrix, the summation of the absolute values for the factor loading coefficients of traits on vectors 2–6 functionally represents the proportion of variance attributable to multivariate "shape" for each trait (Fig. 7A). "Shape" variance, in this sense, is defined as (usually) variance that is subordinate and orthogonal to "size," or the residual variance after the general-size allometric function is divorced from the matrix. Thus the summed coefficients across vectors other than 1 can be taken to represent shape, in as much as vector 1 actually represents a true approximation of theoretical general-size factor for the matrix. This is quite important from the view point of multivariate evolution, because such models generally assume that genetic covariance matrices are static and involve little or ideally no changes in "shape" over short periods of evolutionary time. Functionally, it is relatively easy for groups that differ only in "size" to evolve "apart" in response to selection; all that is required is a differential, allometric evolutionary response to selection where the differing group means slide away from one another, up or down a multivariate regression line that represents the general-size factor. This kind of evolutionary response does not change "shape" because it does not modify the slope or relative elevation of the allometric multivariate regression line in *n*-dimensional evolutionary space.

In contrast, evolving a difference in "shape" requires expending considerably more "evolutionary energy." This is because the elevation and/or slope of the multivariate regression in space must be changed by disruptive and stabilizing selections, which realign the genetic correlations among characters on the shape vectors that are orthogonal to the general-size factor. The amount of difficulty involved in shape evolution depends on the strength of disruptive selection, the amount of pleiotropic linkage for those traits being selected, and the degree of stabilizing selection exerted upon the character suite involved under selective pressure (see Zeng 1988).

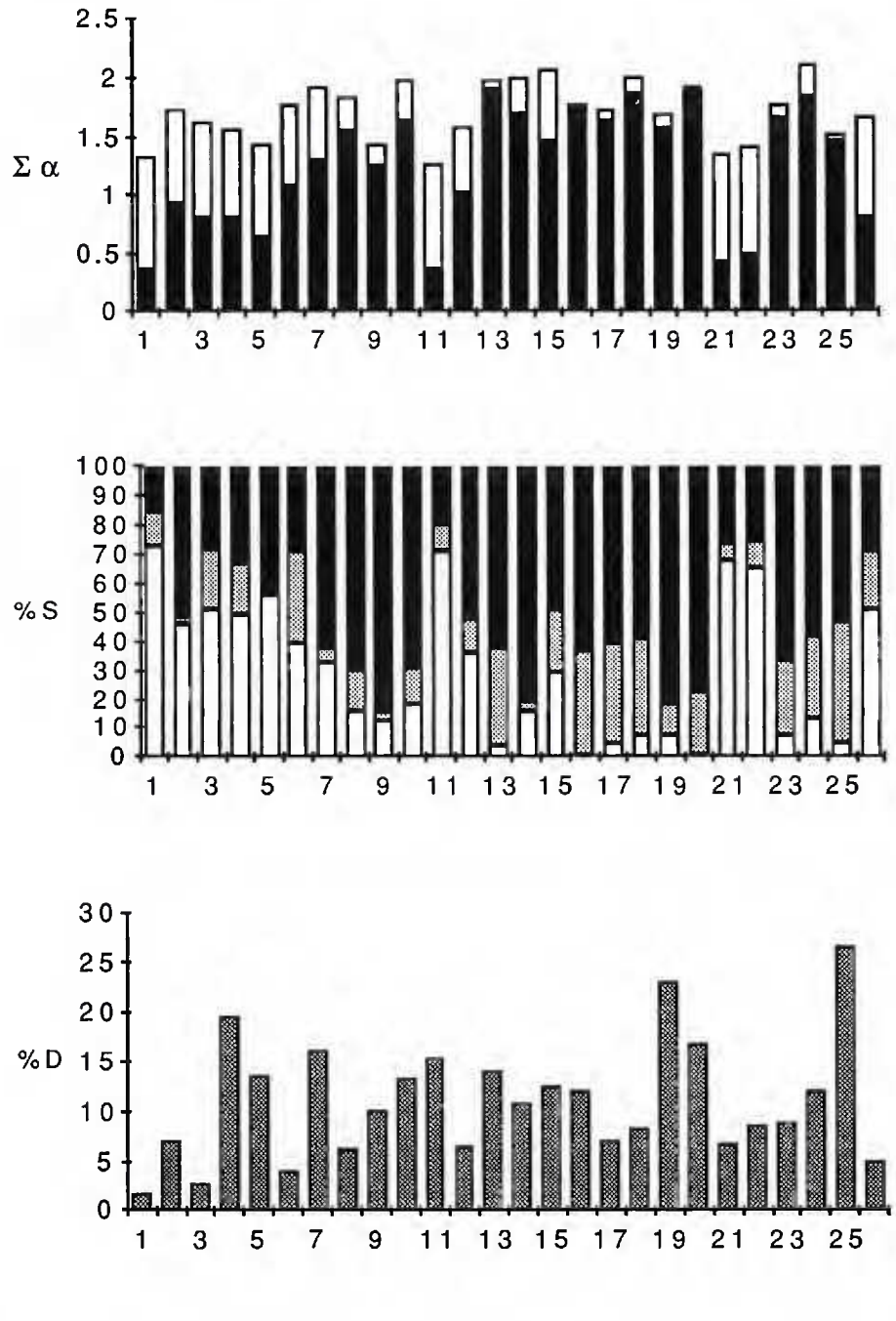

Figure 7. Histograms for *Pseudessigella* indicating: (A) the relative contributions of multivariate "shape" (black), as the summed absolute values of the vector loading coefficients [α] for vectors 2–6, and "size" (white) as the absolute values of vector loading coefficients for the traits on vector 1; (B) the scaled contribution of each trait, as a percentage of size/shape [S], to size vector 1 (white), shape vectors 2 and 3 (gray), and shape vectors 4–6 (black); (C) "uniqueness" among the traits, as the percentage of their differentiation [D], derived as the reciprocal of communality (an indication of the degree of genetic linkage) for the traits.

The cost of shape evolution is indicated by Lemen & Freeman (1984), who note that differing bat genera within the Phyllostomidae are quite conservative for intrageneric shape variance. In those genera intrageneric shape averaged only 1.5% of total variance, while size averaged 35%. The conservation of shape change is further demonstrated intraspecifically by the conclusions of Holman & Kindlmann (1987), whose data indicate that shape changes are ontogenetically fixed between instars of the pea aphid, *Acyrthosiphon pisum* (Harris), in the allometry of the developing antennal and leg segments.

In *Pseudessigella,* the summarized "shape" variance among traits varies considerably, as depicted by the "skyline" atop the black bars in Fig. 7A. This figure shows the stacked summation of each trait's absolute loading coefficients for all vectors. The white bar component for each trait shows the character's size con-

tribution, and the overall "skyline" atop the white bars shows the degree of total contribution by each trait to the overall variance represented by vectors 1–6 (80% of the total variance). Traits that load high on vector 1 (Fig. 5A) generally have larger proportions of white to black in Fig. 7A. These traits, which tend to be segmental lengths, form a character group which isolate on vector 1 (Fig. 5A); they are strongly linked pleiotropically and basically respond to selection for allometric size variation. Other traits that load heavily on vectors 2–6 (Figs. 5B–C, 6A–C) show a much higher ratio of shape to size in Fig. 7A; for example, note that trait 25, metabasitarsus length, and trait 20, the length of caudal setae, among others, show predominantly shape variance.

Because Fig. 7A shows that the traits differ in their absolute contributions to the variance sequestered among the vectors, Fig. 7B was created to more easily portray how the relative contributions of each trait are partitioned. The contributions in Fig. 7B are scaled to 100%. Again, the vector 1 general-size contribution is white, but the shape components (Fig. 7B: nonwhite) are partitioned into the contributions of vectors 2 + 3 (Fig. 7B: gray), and those of vectors 4–6 (Fig. 7B: black). Because each subsequent eigenvector decreases in its proportion of total variance in the data matrix, vectors 2 and 3 together represent 27% of the overall variance, after the 34.1% from size vector 1 is accounted for; the three less dominant shape vectors, 4–6, together account for an additional 22.9% of the variance. All other shape vectors that are potentially extractable from the matrix used (19 more beyond vector 6, [as character $n - 1$]) together account for the remaining 20% of variance in the matrix.

Figure 7C shows the proportion of "uniqueness" (differentiation) as a percentage for each character. In this sense, the uniqueness variance is defined as the reciprocal of communality, which is the variance component for a character that is attributable to common factors (Sneath & Sokal 1973). Genetically, communality entails the variance attributable to pleiotropy or other linkage mechanisms between traits; this operationally assumes environmental effects (including measurement errors) are null, as do most quantitative genetic models. Thus, uniqueness is a measure of the independence of the variance of a character, after its linkage correlations are removed. This independence can result from genetic discord, sampling (measurement) error or, of course, environmental variances which are operationally assumed to be zero here. Note that because the vectors here are derived from PCA rather than discriminant function analysis (DFA), the communality referred does not represent plesiomorphy in the sense of Sorensen (1987a, b) and Sorensen & Sawyer (1989), because PCA does not divorce the information common among groups to provide apomorphy, in the sense of group-divergence information, as does DFA when calculating intergroup Mahalanobis' distance using the Wilks-λ criterion. Because of this important difference, the present figures differ from similar histogram portrayals of variance used elsewhere (Sorensen 1987b: fig. 3, Sorensen & Sawyer 1989: fig. 5) to show the character contributions of apomorphic anagenic distance between groups.

Predictive statements can be made for trait interaction during evolution in eulachnine aphids by comparing the summarized information contained in Figs. 7A–C. Such predictions, however, are based entirely upon the intraspecific variance within *Pseudessigella,* and are dependant upon the stability of the traits that is shown across the genera in the subtribe. This stability is a function, at least in

part, of the genetic independence of the traits (e.g., Fig. 7C), in response to both the disruptive and stabilizing selection pressures that act upon them. Because the information in Figs. 7A–C is multivariately based, however, it should be a better estimator of character interactions during evolution than simple bivariate comparisons of correlations between traits would be; the latter involve a nonmultivariate approach that has been shown to be inferior to multivariately based information in assessing the evolutionary interplay among traits (Willig et al. 1986). Comparing Figs. 7A–C, several observations can be made. For example, of characters 1–7, which show strong general-size affiliation, characters 4, 5 and 7 show relatively elevated levels of uniqueness and are thus assumed to be under less strong genetic linkage; they may, therefore, be more prone to successful disruptive selection. Of characters 2 versus 3 (length of antennal segment V versus the processus terminalis, respectively), 3 shows slightly more total variance of which more is attributable to shape parameters (Figs. 7A, B), although it also shows less genetic independence (Fig. 7C) than trait 2.

Consider the implications for interaction of traits 25 and 26 (metabasitarsal and metadistitarsal length, respectively), during evolution. In comparison to trait 26, trait 25 shows slightly less total contributed variance on vectors 1–6 (Fig. 7A), but its shape influence is larger and thus is more general-size independent; it also shows the greatest level of uniqueness, due to less linkage, of any of the 26 analyzed traits. The metabasitarsal to metadistitarsal ratio shows significant variance throughout the Cinarina and Eulachnina (Mamontova 1972) and within *Essigella* (Sorensen 1983, 1988, unpublished data); previous interpretations of polarity for the interaction of these traits has been questioned (Sorensen 1990). The expression of the variance relationships of the tarsi in *Pseudessigella* is important to potential interpretations for these characters within *Essigella.* By inferring from *Pseudessigella,* if the metatarsal ratio were to evolve differentially among species-groups within *Essigella,* as it has (unpublished data), the metabasitarsus would have necessarily had to undergo shape related evolutionary change via disruptive selection, while the change in the metadistitarsus should be more size related. Although evolution of the metabasitarsus would be more difficult because of its shape variance, it might on the other hand be more easily accomplished because of its lower apparent linkage.

If selective pressure were applied to the metabasitarsus, vector 2 (Fig. 5B), as the suite upon which it loads most heavily, shows that of the linkages that do exist for this trait, it would necessarily have to respond in the most similar fashion to changes in traits 13, 16–18, and 24 (the length of the metanotum [13], the number of dorsal [16] and marginal [17] setae on abdominal terga II–IV and abdominal tergum VIII [18], and the length of ventral setae on the metatibiae). Alternatively, however, if selective pressure were applied to this suite of traits, the metabasitarsus would be the most likely of any of the traits to respond in discord, becoming unstable because of its lower linkage. Disruptive selection would, therefore, most easily act upon this trait.

Character Groups Defined by Multiple Vectors of Shape Selection.—Figures 8A and 8B show the 26 traits in the three-dimensional evolutionary I-space that is generated by the dominant three shape vectors, 2–4. These figures show the same scattergram, but it is rotated 90° in yaw to demonstrate character separation. The original, unrotated, orthogonal vectors were used to define the evolutionary space

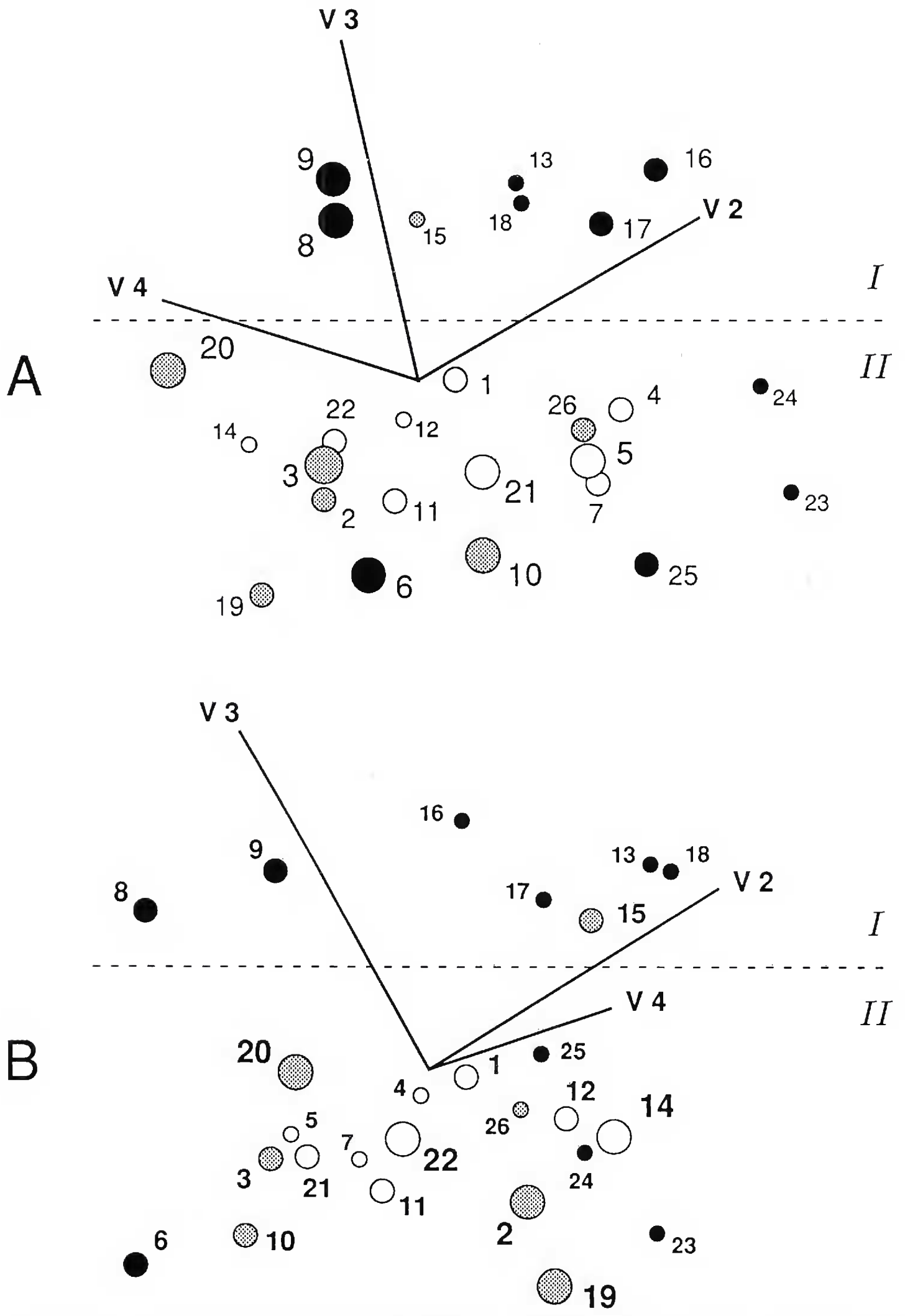

Figure 8. Character groupings for *Pseudessigella* apparent in the evolutionary space defined by a combination of vectors 2–4, as the dominant shape components. Perspectives (A) and (B) represent the same scattergram rotated 90° in yaw. The relative size of each dot and its number shows the relative depth of the point in the third dimension (depth perpendicular to the page). The apparent "groupings" of characters (I and II) are divided with dashed line for emphasis. Traits are assigned to

shown, but the space itself was then rotated to the perspectives depicted. The I-space shown portrays the dominant selective pressure gradients that act upon shape as a component of character variance; it represents 35.9% of the total variance within the *Pseudessigella* matrix, after the elimination of the 34.1% of general-size related variance.

The vectors in Fig. 8 are indicated as intersecting lines, where the distal (labeled) end represents the most positive coefficients on the vectors, and the vector intersection point represents a zero loading coefficient. Note that for this three-dimensional space, as a multivector selection regime for shape, trait 1 occurs the closest to the vector line intersection in both the A and B perspectives. In contrast, traits 12 and 4 also appear close in perspectives A and B, respectively, but are clearly not adjacent to the vector line intersection in the alternative perspectives. Because the location of that intersection represents a zero loading coefficient on all three shape vectors shown, trait 1, overall body size, as the most influential trait in the general-size suite (Fig. 5A) shows almost no residual shape component variance. In contrast, those traits with the highest rank for shape on vectors 2 or 3 occur mostly along the periphery of the distribution field shown.

In Fig. 8, the traits have been ordered into three ranks, showing their relative importance, as drivers, derived from the absolute value of their loading coefficients on the vectors. Although the I-space defined in Fig. 8 represents vectors 2–4, the rank assigned to each trait is the best rank (lowest rank number) that the trait achieved on either vector 2 or 3, as the two most dominant shape vectors. Under this criterion, traits 6, 8, 9, 13, 16–18, and 23–25 have the highest shape influence; traits 2, 3, 15, 19, 20 and 26 are intermediate; and traits 1, 4, 5, 7, 11, 12, 14, 21 and 22, are lowest in shape influence.

The perspectives shown in Fig. 8 depict two character groups are apparent as rough, flattened, somewhat oblong "disks," each with a horizontal orientation; these groups are labeled I and II in the figures. The disks demonstrate that the 26 traits are not randomly distributed in this three-dimensional I-space, rather the characters apparently separate into two "affiliations" as seen from these perspectives. These trait distributions reflect their responses to selection pressure imposed upon them by the vectors as multiple gradients of net natural selection for shape change in multivariate evolution. The relative rankings of the traits are also nonrandomly distributed in this space. Note that character group I has a preponderance of the Rank I characters (6 of 10); group II contains all (9) rank III traits and nearly all (6 of 7) rank II traits as well. If the traits or their rankings were distributed between these groups randomly, group I would be expected to have 27% of the traits in each rank, or 2.7, 1.9 and 2.4 traits from ranks I–III, respectively. The evolutionary meaning of these perspective-dependant character affiliations, if any, is unclear.

Character Stability During the Evolution of Essigella.—Because *Pseudessigella* is the nearest approximation to a progenitor of *Essigella,* and because (except for mutation) variance must be present for selection to result in evolution (Mayr

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one of three ranks determined by the relative importance of their contributions to the shape variance sequestered by vectors 2 or 3: rank I (black)—traits with the highest shape variance; rank II (gray)—traits with intermediate shape variance; rank III (white)—traits with the lowest shape variance.

1963), it was postulated that the pattern of variance for traits shown between groups within *Essigella* should also theoretically occur as intraspecific variance among those traits in *Pseudessigella.* This would imply somewhat stable genetic covariance matrices between these genera, as operational mother and daughter groups (sensu Sorensen 1987a). To explore this hypothesis the dominant shape traits occurring on vectors 2 and 3 were analyzed and ranked for *Essigella, E. kathleenae* and *E. kirki,* as was done for *Pseudessigella.*

Figure 9 shows these character shape rankings, as color codings, for these taxa was well as *Pseudessigella.* The relative degree of shape instability among the taxa can be deduced from Fig. 9 by comparing the color codings of the traits between the taxa. In that figure, stable traits, regardless of their ranking, maintain their color between taxa; moderately stable traits, which change their ranking by only one rank, are shown by white/gray or gray/black color changes between taxa; unstable traits, which change their ranking by two ranks, are shown by white/black color changes.

In comparison to *Pseudessigella,* less than half of the traits on vectors 2 or 3 remained stable during the evolution to *Essigella.* Traits 16–18, 23 and 24 remained unchanged in rank I (Fig. 9: black) as attributes high in shape variance on vectors 2 or 3. Traits 1, 11, 12, 14, 21, and 22 were unchanged in rank III (Fig. 3: white), but no traits remained unchanged in rank II (Fig. 9: gray). Several traits, however, changed dramatically between the genera: trait 7 changed from rank III (Fig. 9: white) in *Pseudessigella,* from poor in shape variance, to rank I in *Essigella*; traits 6, 9, 13 and 25 behaved the opposite. Many traits (2–5, 8, 10, 15, 19, 20, and 26) changed only one rank, in various directions, between the genera. Thus, between *Pseudessigella* and *Essigella* nearly 42% of traits (11 of 26) are stable with regard to shape variance; 39% (10 of 26) show moderate stability, and 19% (5 of 26) are unstable.

Note that in *Essigella* the metabasitarsus, trait 25, has apparently changed shape from its variance in *Pseudessigella,* becoming unstable and moving from rank I to III. The metabasitarsus, therefore, has decoupled in part from the other dominant traits, 16–18 and 24, in the suite represented by vector 2 (Fig. 6B) in *Pseudessigella.* The same is true for trait 13, although the latter showed considerably less independence in *Pseudessigella* (Fig. 7C). Unfortunately, stability in evolutionary traits remains more easily observable than predictable.

Figure 9 also shows the shape component rankings for *E. kathleenae* and *E. kirki.* For *E. kathleenae,* traits 17, 18 and 23 are rank I; traits 2, 3, 6, 7, 9–11, 15, 19, 20, 22 and 24 are rank II; and traits 1, 4, 5, 8, 12–14, 16, 21, 25 and 26 are rank III. For *E. kirki,* traits 3, 4, 6, 10, 14, 16, and 18 are rank I; traits 2, 5, 8, 20 and 23–25 are rank II; and traits 1, 7, 9, 11-13, 15, 17, 19, 21, 22 and 26 are rank III.

The similarity of shape component variance among all the taxa was calculated for taxon-pairs and represents a measure of shape stability during evolution (Fig. 10). *Pseudessigella* and *Essigella* have a shape similarity of 0.62. *Essigella kathleenae* shows the greatest degree of shape stability in common with *Pseudessigella* (0.71), more so in fact than with *Essigella* (0.67); *E. kirki* has an equal degree of shape stability (0.62) with either genus. Interestingly, however, shape stability between *E. kathleenae* and *E. kirki* (0.60), both group I species, is lower than that between either species versus either genus. These values suggest that *E. kirki* has

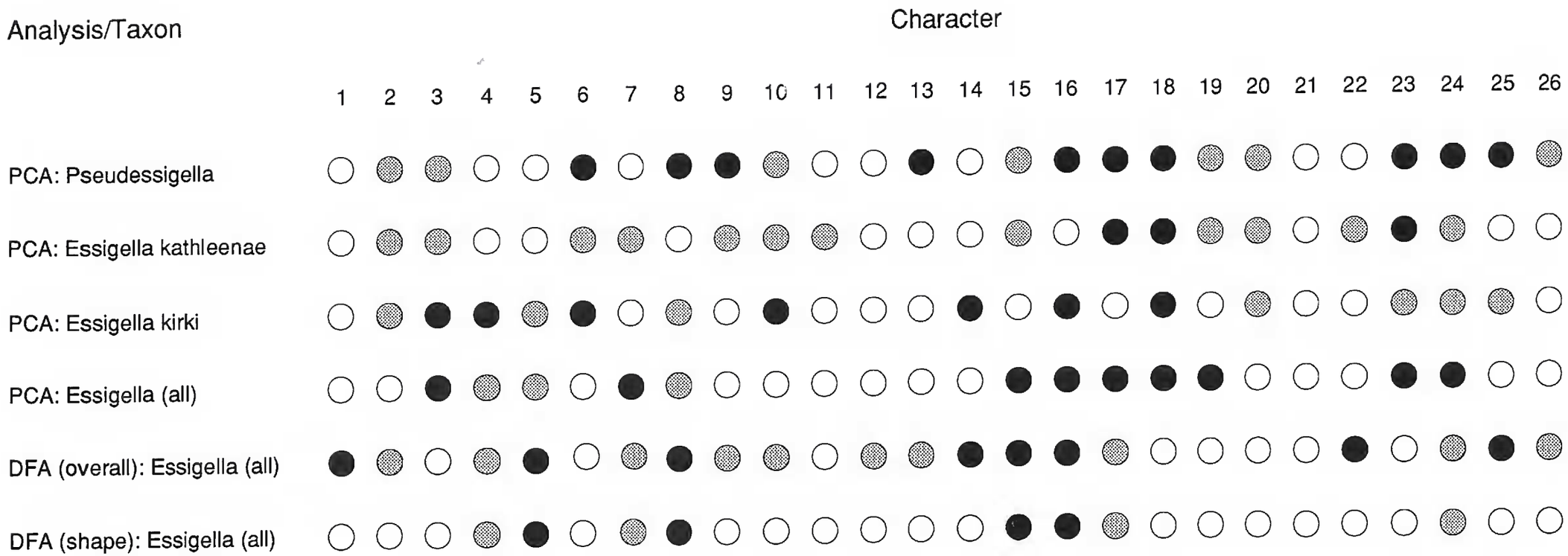

Figure 9. Relative ranking and stability of the shape component variance for each trait on PCA vectors 2 or 3 among taxa, and the DFA diagnostic ranking of traits for *Essigella*. For PCAs (either vector 2 or 3): rank I (black)—traits with the highest shape variance; rank II (gray)—traits with intermediate shape variance; rank III (white)—traits with the lowest shape variance. For DFA (overall) (vectors 1-3): rank I (black)—best multivariate separators; rank II (gray)—intermediate multivariate separators; rank III (white)—poorest multivariate separators. For DFA (shape) (vectors 1–3), rankings for "shape-based-diagnostics" are: rank I (black)—trait is a rank I multivariate separator with either rank I or II shape variance; rank II (gray)—trait is a rank II multivariate separator with either rank I or II shape variance; rank III (white)—trait is a multivariate separator of any rank but has rank III shape variance, or trait is a rank III multivariate separator of any rank shape variance.

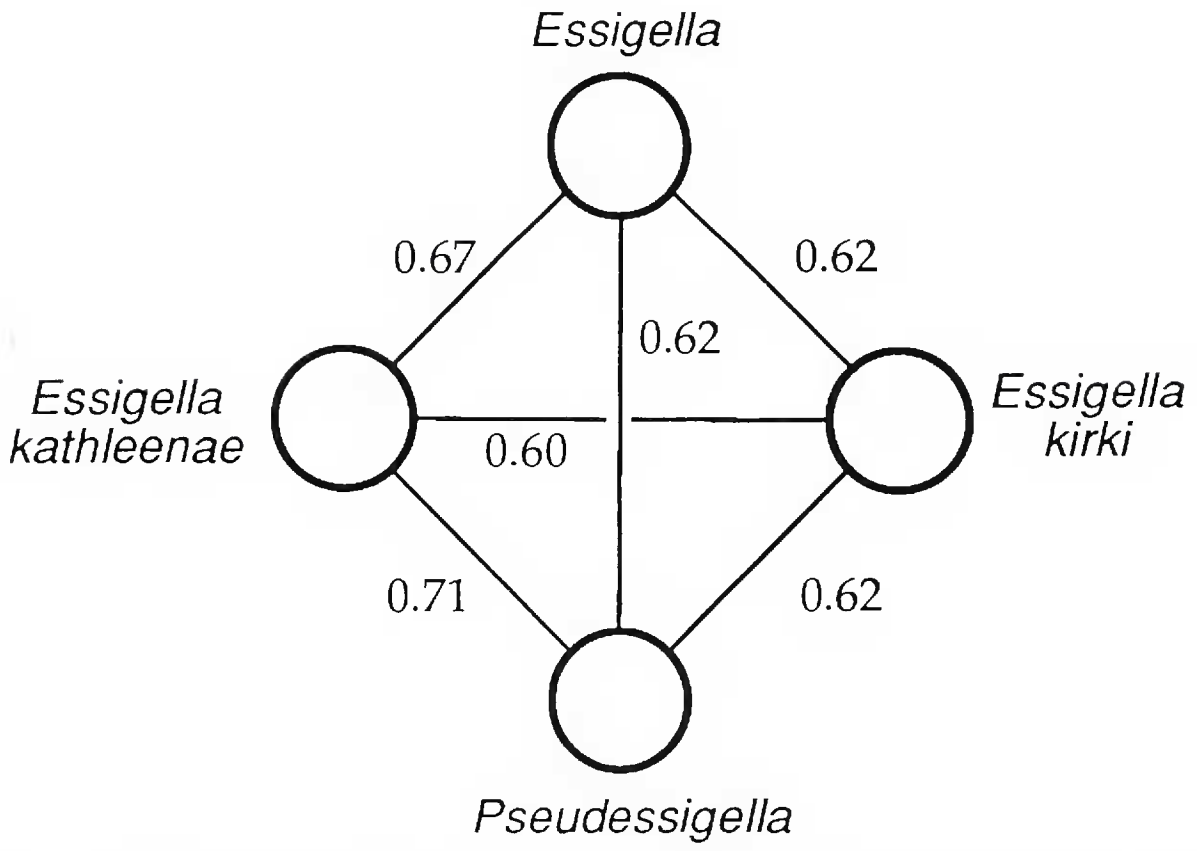

Figure 10. Similarity among the taxa, for shape components on PCA vectors 2/3. The similarity values (= 1 − distance) can be interpreted as an index of the stability of the relative rankings for the shape component of the traits on the two most dominant shape vectors.

had more shape selection imposed upon it than has *E. kathleenae.* It might be considered to be more "wayward" in shape, along a possible evolutionary "shape" continuum between the genera. This is despite previous findings that *E. kirki* was the closest in total anagenic distance to *Pseudessigella* on the phylogenetic network for these taxa and, therefore, represented the most primitive *Essigella* species (Sorensen 1987a).

The variance shown in shape stability between the taxa also indicates shape components may not, therefore, be as stable during multivariate evolution as might be thought, at least within the Eulachnina. Stabilizing and disruptive selection among the covariant character suites may be rather important during multivariate evolution, both within *Essigella* and between it and *Pseudessigella.* Because orthogonal shape is more theoretically conservative as a phylogenetic component during the evolution of a genus than is size (Leman & Freeman 1984), one would expect that shape variance should also be more important between differing groups of species, as clades, within a genus also (e.g., species-groups and monophyletic subgenera). Variance in shape components between species within a genus should occur mostly at the species-group level or above, because of the more significant evolutionary effort required to modify differing orthogonal character suites. In contrast, the differences between species within species-groups or complexes should most efficiently evolve by simple allometric change along their common general-size component; this would suggest that monophyletic species-groups should show mostly size differences between their closely related species, subspecies, etc.

This is not shown, however, between the group I species here. Using this logic, if *E. kathleenae* and *E. kirki* were parts of a tight monophyletic group, they should have shown a higher similarity in shape variance, with their major differences

occurring in general-size variance. Because group I of *Essigella* is paraphyletically defined and plesiomorphically sequestered within genus (Sorensen 1987a), however, the relatively low stability in shape between these species is not that surprising. They do not form a clade and because of their early "divorce" from each other and the remaining *Essigella* lineage(s), they have the least phyletic commonality of any pair of species in the genus. Although they are phenotypically quite similar, their similarity is largely based in plesiomorphy with reference to other *Essigella.*

Because both the size and shape components of traits should be important during radiant evolution of species within a genus, a DFA of all species of *Essigella* was conducted to explore which traits that are highest in shape variance are also the most multivariately important in differentiating monophyletic groups (clades) within the genus. Because the functions of DFA represent Landean minimum selective mortality measures (as: $[\nabla \ln \bar{W}]^{T}z$, sensu Lande 1979), they are parsimonious indices of the apomorphic anagenic distance that is necessary to account for the observed contemporaneous positions of the group centroids for the species in the *n*-dimensional space defined by the DFA vectors (Sorensen 1987a, b; Sorensen & Sawyer 1989). In this context, the vector loading coefficients of the characters on the functions determine the relative importance of each trait as a parsimonious contributor to the observed evolution (separation) of species for the matrix employed.

The results of the DFA are also shown in Fig. 9. Traits 1, 5, 8, 14–16, 22 and 25 in rank I have the highest multivariate contributions in optimally distinguishing (and evolving, sensu Lande 1979) *Essigella* species. Traits 2, 4, 7, 9, 10, 12, 13, 17, 24 and 26 show intermediate multivariate importance in rank II, and traits 3, 6, 11, 18–21 and 23 have the least importance in rank III. From these results, it is apparent that a mixture of traits that show their strongest variance in both size and shape seem important in the overall historical evolution of *Essigella* species.

To determine if traits with high shape variance (present criteria) best multivariately distinguish groups of species, as clades, within *Essigella* rather than individual species within such groups, a new set of rankings was created (shape-based-diagnostics) to reflect both the multivariate contribution of each trait as a diagnostic in DFA, and the relative importance of its shape contribution in *Essigella.* Three ranks were assigned (Fig. 9): rank I traits were the best (rank I) separators in DFA that also had either the highest or intermediate shape variance (ranks I or II) in PCA; rank II traits were intermediate separators (rank II) in DFA which also had either the highest or intermediate shape variance (ranks I or II) in PCA. Rank III traits were poor DFA separators (diagnositc rank III) of any shape rank, or were either the best or intermediate rank separators (diagnostic ranks I or II) that showed poor shape variance (shape rank III).

As rank I shape-based-diagnostics, traits 5, 8, 15 and 16 appear to best separate groupings of species within *Essigella* rather than simply individual species (Sorensen 1983). Trait 16, the number of dorsal setae on the terga of the anterior abdomen segments, separates the three major groupings of *Essigella* (Sorensen 1987a: groups I, II, III); groups II and III care clades, as is the combination of II + III. Trait 16 also differentiates *E. pini* Wilson homoplasiously from the monophyletic species-group involving *E. californica* and *E. hoerneri* (Sorensen

1987a: spp. H, A, B, respectively), within group III. Trait 8, a body width component, separates the monophyletic species complex involving *E. knowltoni* Hottes (Sorensen 1987a: spp. E, F, G) and to a lesser extent its monophyletic cohort *E. alyeska* Sorensen (Sorensen 1987a: sp. D), as a clade within group III; this assemblage involves a major portion of the orthogonal shape covariance shown among the species of group III. Trait 15, the maximal length of a set of sclerites that serve as muscle anchorages on the venter of the anterior abdominal segments, serves to separate many clades within *Essigella,* notably: group II, the *E. knowltoni* complex of group III, and the *E. californica* complex of group III. Trait 5, the length of the third antennal segment, shows both size and shape variance; it separates the *E. californica* complex as a clade, and also separates individual species within several other species-groups.

As rank II shape-based-diagnostics, traits 4, 7, 17 and 24 are less apparent in distinguishing groupings above the species level (Sorensen 1983). Trait 4, the length of the fourth antennal segment, behaves much as trait 3 in that some groupings of species show differential expression for the segment (e.g., group II, and some complexes within group III) to a degree, but the trait varies between species within some species-groups (e.g., the *E. knowltoni* complex of group III). Traits 7 and 24, the length of setae on the frons and ventral setae on the metatibia, are more difficult to interpret because of homoplasy and intraspecific variance. Both sets of setae have characteristic patterns of variance within species; they are always (plesiomorphically ?) short in some *Essigella* species (e.g., *E. kathleenae* and *E. kirki* of group I), but can vary widely in their lengths among individuals of other *Essigella* species (e.g., the *E. knowltoni* and particularly the *E. californica* complexes of group III) showing an apomorphically longer mean setal length for such species. Trait 17, the number of marginal setae on the anterior abdominal segments, parallels trait 16 and shows the same group defining properties, except that the variance in trait 17 is slightly more within several species.

Rank I shape-based-diagnostics, as a class, therefore, appear to best distinguish clades at various levels within *Essigella,* more than individual species within those groupings. Rank II shape-based-diagnostics, however, appear less evident in their separation of clades rather than individual species, and these traits tend to show variance that is either more homoplasious between species(-groups) or is subject to intraspecific variance in *Essigella.*

Traits within *Essigella* that are rank I diagnostics, exclusive of those that are also rank I or II shape-based-diagnostics, should be expected to portray higher levels of (homoplasious) importance in separating species within species-groups. Because the analysis of such size-based-diagnostics requires a local partitioning of the overall variance within *Essigella* at the level of its species, the examination of size-based-diagnostics will be treated elsewhere (unpublished data).

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